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Among-year and within-population variation in foraging distribution of European shags *Phalacrocorax aristotelis* over two decades: Implications for marine spatial planning

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ABSTRACT

Marine spatial planning aims to deliver sustainable use of marine resources by minimizing environmental impacts of human activities and designating Marine Protected Areas. This poses a challenge where species' distributions show spatio-temporal heterogeneity. However, due to logistic constraints and challenging timescales many studies of distribution are undertaken over few years or on a restricted subset of the population. Long-term studies can help identify the degree of uncertainty in those less comprehensive in space and time. We quantify inter-annual and sub-colony variation in the summer foraging distribution of a population of European shags *Phalacrocorax aristotelis*, using a tracking data set comprising 320 individuals and 1106 foraging trips in 15 years from 1987 to 2010. Foraging distribution over the study period was concentrated in three areas. Data from one and two years captured an average of 54% and 64% of this distribution, respectively, but it required 8 years' data to capture over 90% of the distribution. Foraging range increased with population size when breeding success was low, suggesting interplay between extrinsic and intrinsic effects. Furthermore, females had foraging ranges on average 36% greater than males. Finally, sub-colony segregation occurred in foraging areas up to 4 km from the colony and in the most distant locations (>10 km), whilst there was considerable overlap at intermediate distances (6–10 km). Our study highlights important considerations for marine spatial planning in particular, and species conservation in general, notably the proportion of the population distribution identified, the prevailing conditions experienced and the need for balanced sampling across the population.

1. Introduction

The growing concern about the negative effects of human activities on marine wildlife underpins the goals of marine spatial planning, whereby sustainable use of marine resources is sought by integrating conservation and economic interests (Douvere, 2008). Within this framework, two important conservation measures are to ensure that new developments such as marine renewables are designed and located to minimize impacts on protected species, and to designate the most important areas for wildlife as Marine Protected Areas (MPAs; Claudet, 2011). For top predators such as seabirds, identifying important areas is challenging because at-sea distribution may vary with environmental conditions (Louzao et al., 2009) and intrinsic mechanisms at the population level (e.g. density dependence, Lewis et al., 2001) or individual level (e.g. sex, Quintana et al., 2011). Furthermore, different components of a population may vary in distribution. For example, individuals from sub-colonies may segregate at sea driven by energetic constraints, competition or use of local information (Hipfner et al., 2007).

An increasingly widespread method of quantifying important areas for seabirds is the deployment of tracking devices on breeding individuals at colonies (Burger and Shaffer, 2008). However, despite the potential for considerable temporal and spatial

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heterogeneity in at-sea distributions, tracking studies of breeding seabirds are often carried out in a small number of years because of challenging timescales to deliver results and in restricted locations within the colony because of logistical constraints. Some of these studies have been strengthened by integrating tracking data with at-sea survey data, and incorporating modeling of habitat association of seabirds to predict distributions (e.g. Louzao et al., 2009). However, the risk is that important foraging areas are being identified based on a narrow set of conditions, potentially jeopardizing their effectiveness in the long term. Furthermore, potential sub-colony effects have largely been ignored yet may be of fundamental importance, since they will determine what proportion of a population is likely to be protected by MPA designation or affected by an anthropogenic development.

To identify important areas for breeding seabirds that consider this spatio-temporal heterogeneity, it is crucial to quantify a population's foraging distribution over a number of years and for different sub-colonies. Furthermore, it is important to determine how environmental conditions or intrinsic mechanisms underpin this variation. Tracking with data loggers is the most appropriate method for assessing distribution of seabirds of known colony origin and breeding status. However, few long-term tracking studies on seabirds exist (Phillips et al., 2008; Weimerskirch et al., 2012; this study). By quantifying among-year and within-population variation in distribution, and the environmental and intrinsic drivers of this variation, such studies can help identify the degree of uncertainty in conclusions drawn from studies where the number of seasons and/or coverage of the colony are limited.

Here, we quantify inter-annual and sub-colony variation in foraging distribution of European shags *Phalacrocorax aristotelis* (hereafter "shags") from the breeding colony on the Isle of May off the coast of south-east Scotland using a tracking data set spanning more than two decades during which environmental conditions, population density and diet composition varied considerably. The species is endemic to the northeast Atlantic. In the UK, it has been in decline for over a decade (JNCC, 2013) and is amber listed as a species of conservation concern (Eaton et al., 2009). As an inshore-feeding, pursuit-diving seabird, the shag may be affected by tidal and wave renewable energy developments (Grecian et al., 2010; Langton et al., 2011). Important areas, including those used for foraging, are potential candidates for designation as Special Protection Areas (SPAs) under the EU Birds Directive (EU, 2009). Therefore, detailed information on foraging distribution is important for the effective identification of protected areas and assessment of potential impacts of human activities. We use our long term tracking data set to: (1) quantify the consistency of important foraging areas across years; (2) assess the minimum number of years of data collection needed to provide a robust estimate of the long-term population foraging distribution; (3) identify extrinsic and intrinsic determinants of foraging range and (4) quantify sub-colony segregation in foraging distributions. We use our results to highlight factors marine spatial planners should consider when making decisions based on less comprehensive data sets.

2. Methods

2.1. Field site and data collection

The study was carried out on the Isle of May National Nature Reserve, south-east Scotland (56°11′N, 2°33′W). Foraging locations of adult shags were obtained using animal-borne instrumentation in 15 breeding seasons over the period 1987–2010. Four methods involving three types of devices were used to estimate foraging location: dead-reckoning from VHF telemetry, triangulation from VHF telemetry, dead reckoning from compass loggers and GPS tracking (Wanless et al., 1991, 2005; see online Appendix A1 for full details). All data were collected during the chick-rearing period except in 2001, when foraging trips during incubation were also recorded. Birds were captured at the nest using a crook, and the tracking device attached to back or central tail feathers using waterproof tape (Tesa Ltd.) and/or cable ties. Birds typically carried devices for short periods (median: 1.2 days; range: 0.6–25 days) before they were recaptured and the device retrieved. No adverse effects were witnessed during capture and handling, and birds returned to the nest within 10 min in all cases where the mate had not assumed nest duties. Device type, sample sizes and deployment period for each year are summarized in Table 1. Birds were sexed by voice and behavior (Snow, 1960).

To explore the effect of density dependence, we used annual breeding population size (number of pairs; Alampo and Ash, 2010), estimated using standardized methods that are employed at seabird monitoring sites in the UK (see Walsh et al., 1995 for data collection protocols). As an integrative measure of environmental conditions (Frederiksen et al., 2007) we used population breeding success, which was the average number of chicks fledged per pair recorded each year in a sample of nests (mean: 142; range: 60–288) using standardized methods (Walsh et al., 1995). The effect of diet composition, as an indicator of availability of different prey, was also explored. Diet composition was determined from food regurgitated by chicks and adults collected opportunistically during fieldwork (samples per year: mean: 37; range: 16–64), from which annual biomass proportions of each diet species was

Table 1
Annual deployment summary over the study period, including original sample size of foraging locations and subsampling of GPS data to enable comparison across years (see main text).

Year	Device type	Deployment period	*n* Birds	*n* Foraging trips	*n* Foraging locations	*n* Subsampled foraging locations
1987	VHF	28 June–24 July	10	NA	139	139
1988	VHF	29 June–17 July	12	NA	85	85
1989	VHF	10 June–5 July	7	NA	106	106
1990	VHF	2 July–8 July	15	23	27	27
1991	VHF	12 July–21 July	24	29	43	43
1992	VHF	1 June–18 July	43	100	159	159
1994	VHF	9 July–22 July	9	41	60	60
1997	VHF	30 May–30 July	41	41	41	41
1998	VHF	22 June–31 July	19	19	19	19
2001	VHF	17 May–7 July	41	48	48	48
2002	Compass	4 June–30 June	16	31	61	61
2003	GPS	1 June–11 June	10	32	1181	50
2008	GPS	19 June–24 June	9	21	1934	42
2009	GPS	3 June–23 June	31	202	8379	469
2010	GPS	8 June–24 June	33	260	7621	463
Total			320	1106	19903	1812

estimated (see online Appendix A2 for details). Since the lesser sandeel (*Ammodytes marinus*) dominated the diet overall, but varied in importance between years, we used annual proportion of sandeels in biomass as a proxy of diet composition.

2.2. Data analysis

2.2.1. Interannual variation in foraging areas

Raw data were processed to obtain foraging locations defined as locations where the bird dived (see online Appendix A1 for details). Locations from VHF telemetry and compass loggers were confirmed diving locations. With GPS data it was not possible to distinguish between diving locations and locations on the water surface; however, over 90% of non-flight locations at sea in this population involve active diving (Wanless et al., 2005). GPS loggers recorded much higher numbers of locations than VHF telemetry or compass dead-reckoning. As the older technologies typically recorded one location per foraging bout, we subsampled GPS data by selecting the mean location per foraging bout to make the data comparable across years (sample size of original and subsampled locations shown in Table 1; see online Appendix A1 for bout criterion).

For each year (except 1998, when data were not sufficient), fixed kernel analysis was performed in ArcGIS (Hawth's Analysis Tools 3.27), with a smoothing parameter (h) identified using the least-squares cross-validation method (Worton, 1989; range 1.5–3 km). Core area (area of the 50% kernel contour) and area of active use (area of the 90% kernel contour) were generated in a Lambert equal-area azimuthal (North Pole) projection. Interannual variation in core foraging areas was examined by quantifying the pairwise overlap of 50% kernel contours between years as: $2a_{\text{overlap}}/(a_1 + a_2)$, where a_1 and a_2 are the areas of the two respective kernel contours and a_{overlap} is the area of overlap.

To assess the long-term persistence of foraging areas, the 50% and 90% kernel contours were converted into grids with 1 km^2 cell size and the total number of years in which each grid cell was used was determined.

2.2.2. Minimum adequate sample size

In order to establish the minimum number of years of data collection needed to estimate the foraging area identified from our long-term study we examined the relationship between overall area used (area of the 90% kernel contour) and sample size of years using a resampling procedure. This procedure was performed in R (R development core team, 2012), and involved creating 1000 resampled datasets for each of a range of sample sizes, $n_b = 1, 2, \ldots, n$ (where n denotes the total number of years for which we have data). Each resample was constructed by selecting n_b years at random, without replacement, from the set of n years (Manly, 2009), and a kernel density estimate was then derived from the pooled data from all years within each resample (using the ks package within R). The kernel density estimate for each resample was used to derive the area of the 90% density contour, and the distribution of these areas across the 1000 resampled datasets was used to quantify the typical foraging area associated with n_b years of data. Using this distribution, it was also possible to quantify the uncertainty associated with estimating this area.

As the number of birds tracked varied among years and a larger sample of birds may reflect more reliably the annual population foraging area (e.g. Girard et al., 2002; Soanes et al., 2013a), we weighted each location fix in such a way that each individual bird was assigned the same overall weight. This was achieved by assigning the weight associated with each fix to be $w_i = \phi/f_i$, where f_i is the number of fixes associated with bird i and ϕ denotes the overall mean number of fixes per bird. Thus, years with a larger number of individuals tracked were given larger weight in the analysis.

2.2.3. Extrinsic and intrinsic determinants of foraging range

The effects of extrinsic and intrinsic variables on foraging range were investigated using linear mixed models. The maximum distance from the colony per bird (total $n = 320$) was used as a measure of foraging range, and was the response variable within all models. Maximum distance from the colony was square root transformed in order to achieve approximate normality. The simplest model considered (the 'null model') contained a random effect for 'year' but contained no fixed effects. The most complicated model (the 'full model') contained year as a random effect, five explanatory variables and one interaction term as fixed effects. The five explanatory variables were sex, diet, device type, population breeding success and the square root of breeding population size. The interaction term was sqrt (breeding population size) by population breeding success. Breeding population size was square root transformed to achieve a linear relationship with foraging range, which resulted in a better model fit. The proportion of sandeels in the diet was strongly bimodal, with sandeels either accounting for less than 60% of the diet or for more than 80% of the diet in each year, and was therefore modeled as a binary variable (less than 60%, more than 60%). Device type was modeled as a three level categorical variable (VHF/compass/GPS) to account for potential variation in foraging range arising from different tracking devices used. Sex was included in the models to test for differences in foraging range associated with sexual size dimorphism (Quintana et al., 2011). The interaction between population breeding success and population size was included because density dependent processes can vary with environmental conditions (e.g. Davies et al., 2013). All possible subsets of the variables in the full model were considered, which led to a candidate set containing forty models (8 models that included the interaction term and 32 models that did not). For the purposes of model comparison, models were fitted using maximum likelihood as they had different fixed effects but the same random structure (Zuur et al., 2009). Support for different candidate models was assessed using Akaike's information criterion adjusted for small sample size (AICc) and Akaike weights; see also online Appendix A3. The model with the lowest AICc value (and highest Akaike weight) was considered best supported. Models were deemed strongly supported if they differed from the best model by up to two AICc units (Burnham and Anderson, 2002, p.70), unless they contained one more parameter and had a higher AICc than the best supported model, in which case this rule of thumb is not appropriate (Burnham and Anderson, 2002, p.131); such models were disregarded on the grounds of parsimony. The final model was re-fitted using restricted maximum likelihood to obtain parameter estimates and their standard errors (Zuur et al., 2009). Analyses were performed in R (package nlme).

2.2.4. Sub-colony variation in foraging areas

Shags in this population nest in sub-colonies distributed throughout the island (Barlow et al., 2013). Potential sub-colony variation in foraging areas was explored through simultaneous targeted deployments of GPS loggers in one northern and one southern sub-colony, approximately 1 km apart, in 2009 and 2010. In the years prior to 2009, different sub-colonies were sampled in different years, so it was not possible to disentangle sub-colony from year effects. Therefore, this analysis was restricted to 2009 and 2010. A visual inspection of the data indicated that the spatial distribution of locations from individuals in each sub-colony was similar in the 2 years, so the data were pooled ($n = 39$ and 25 birds for the northern and southern sub-colony, respectively). To quantify overlap between the foraging locations of birds breeding in the two sub-colonies at different distances from the colony, foraging

locations were split into 2 km distance bands from the island's coastline. As very few locations (5% of northern sub-colony and 3% of southern sub-colony) were recorded beyond 12 km from the Isle of May, these were pooled with locations in the 10–12 km distance band. Overlap between 50% kernel contours was calculated for each distance band, using the same methods as for annual kernels.

3. Results

3.1. Interannual variation in foraging areas

Three main foraging areas were used over the study period: (1) the area immediately surrounding the island; (2) an inshore area west of the island, near the mainland coast and (3) an inshore area north of the island near the mainland coast (Fig. 1a and b; for annual plots see online Appendix A4). Areas (1) and (2) were used in all years while area (3) was used in 12 out of 15 years. In contrast, other foraging areas were used more rarely, with the most distant locations used in a single year, 1992, when foraging range was much greater than in any other year (mean maximum range per bird ± SD: 17.7 ± 8.4 km; mean ± SD across the remaining years: 8.4 ± 3.5 km; Fig. 1b; see online Appendix A4; overall mean maximum range 9.0 ± 3.8 km). Annual pairwise overlap of core foraging areas (50% kernel contours) varied substantially (mean 27%; range 0.2–74%; see online Appendix A5 for details).

3.2. Minimum adequate sample size

Randomized sampling indicated a substantial increase of foraging area with sample size up until 8 years, after which the increment with each additional year was less than 2% (Fig. 2). Randomized samples of one, two and three years of data captured 54%, 64% and 71% of the area identified using 15 years of data, respectively; 92% of this area was captured with 8 years of data and 95% with 11 years of data (Fig. 2). When 1992 was excluded

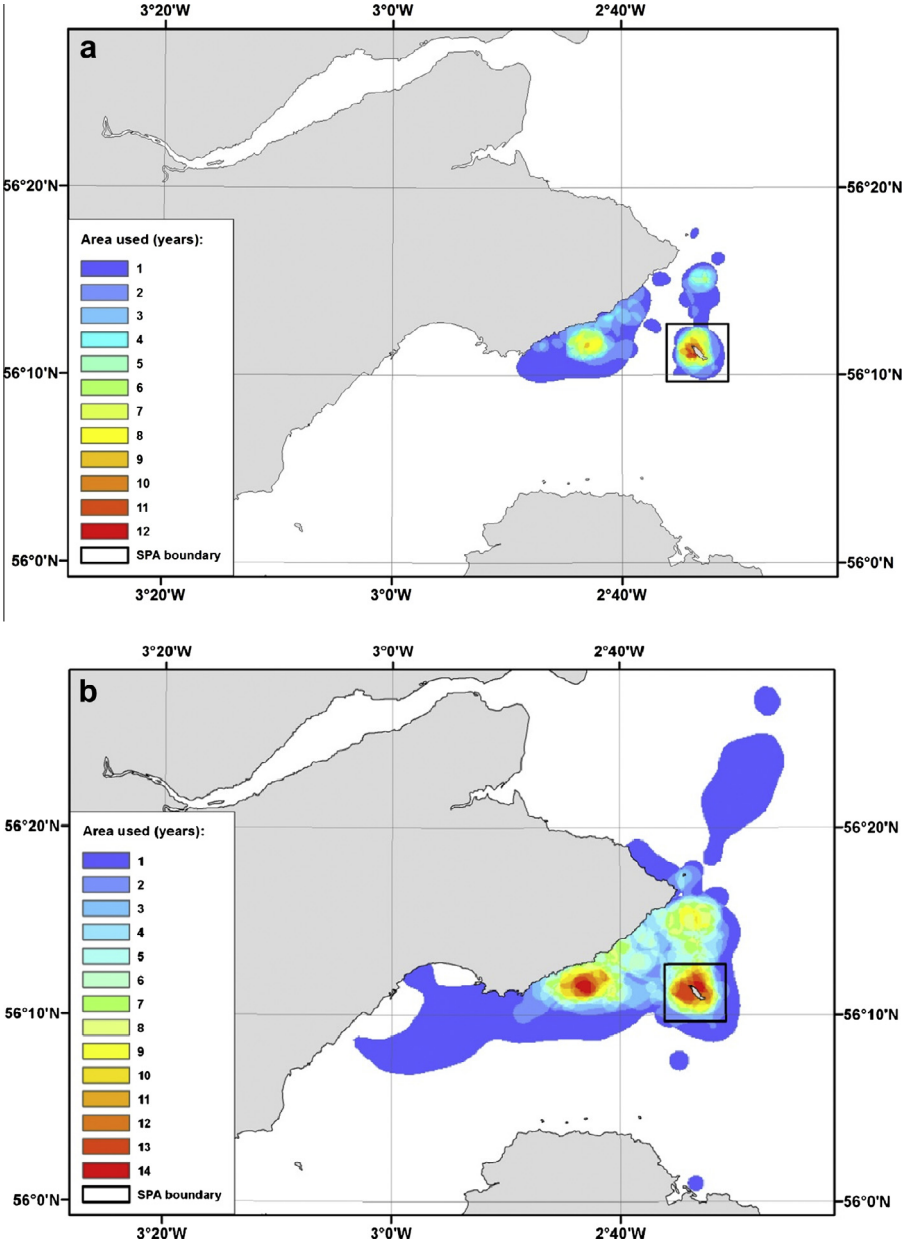

Fig. 1. Consistency in use of 1 km^2 cells within (a) core area and (b) area of active use across years.

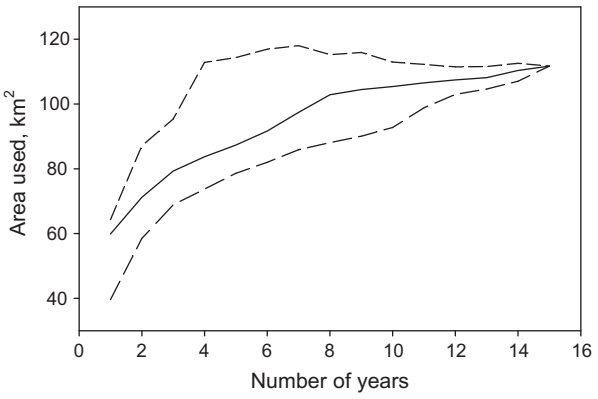

Fig. 2. Relationship between foraging area and sample size of years estimated from a resampling procedure (see Methods for details). Median area (solid line) and 25 and 75 percentiles (dashed lines), shown for each randomized sample size.

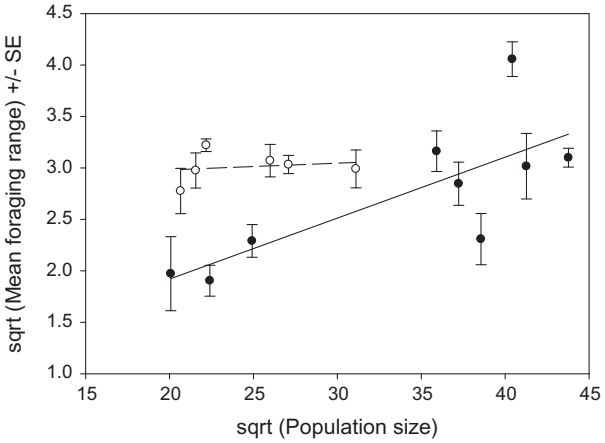

Fig. 3. Interacting effects of population size and breeding success on shag foraging range (see Methods for details). For illustrative purposes breeding success was split into two categories: low (<1.5 chicks fledged per nest; filled circles and solid line on graph) and high (>1.5 chicks fledged per nest; open circles and dashed line). However, the statistical analysis was carried out with breeding success fitted as a continuous variable (Table 2).

from the analysis, the increase in foraging area with sample size levelled off at 6 years. Randomized samples of one, two and three years of data captured 62%, 71% and 78% of the area identified using 14 years of data, respectively; 95% of this area was captured with 10 years of data.

3.3. Extrinsic and intrinsic determinants of foraging range

During the study period, the population showed substantial variation in breeding population size (median of annual estimates: 581; range: 259–1916 pairs), breeding success (median: 1.0; range: 0.2–2.0 chicks/pair) and diet composition (sandeel percentage in the diet: median 95%, range 28–100%; see online Appendix A6).

Foraging range increased with population size when breeding success was low, but not when breeding success was high (Table 2, model 1; Fig. 3), suggesting an interacting effect of population density and environmental conditions. Females foraged further away than males on average, independently of the effects of population size and breeding success (females: 11.4 ± 0.6 km; males: 8.4 ± 0.4 km). The model including the same main effects but no interaction was relatively strongly supported (Table 2, model 3). The model including only population size, population breeding success and the interaction between them was also relatively strongly supported (Table 2, model 5). There was weak evidence for a relationship between diet composition and foraging range (Table 2: since model 2 contained only this additional parameter but had a higher AICc value than the best model this suggested that this variable was not important; a comparison of models 4 and 5 similarly implies weak support). There was no evidence for effects of device type used on our estimates of foraging range (Table A.3.1). The results were qualitatively unchanged when 1992, the year when foraging range was unusually large, was excluded from the analysis.

3.4. Sub-colony variation in foraging areas

Within 2 km of the colony, core foraging areas (50% kernel contours) of shags from the northern and southern sub-colony were

Table 2
Linear mixed models testing for relationships between population size (PS), breeding success (BS), diet composition (Sndl) and sex, and foraging range. Best model shown in bold; only models with relatively strong support (ΔAICc < 4) presented, ordered by AICc (lowest to highest); for full set of candidate models see Table A.3.1. in online Appendix.

Model no	Model	Number of parameters	Parameter estimate ± SE	AICc	ΔAICc	AICc weight
1	**sqrt(PS)+BS + Sex + sqrt(PS):BS**	**6**		**818.6**	**0**	**0.28**
	sqrt(PS)		**0.12 ± 0.04**			
	BS		**2.43 ± 1.00**			
	Sex		**0.22 ± 0.11**			
	sqrt(PS):BS		**−0.07 ± 0.03**			
2	sqrt(PS)+BS + Sndl + Sex + sqrt(PS):BS	7		818.8	0.2	0.25
	sqrt(PS)		0.14 ± 0.05			
	BS		3.04 ± 1.24			
	Sndl		0.39 ± 0.45			
	Sex		0.22 ± 0.11			
	sqrt(PS):BS		−0.09 ± 0.04			
3	sqrt(PS)+BS + Sex	5		821.7	3.1	0.06
	sqrt(PS)		0.05 ± 0.02			
	BS		0.58 ± 0.26			
	Sex		0.23 ± 0.11			
4	sqrt(PS)+BS + Sndl + sqrt(PS):BS	6		822.0	3.4	0.05
	sqrt(PS)		0.15 ± 0.05			
	BS		3.21 ± 1.25			
	Sndl		0.43 ± 0.46			
	sqrt(PS):BS		−0.10 ± 0.04			
5	sqrt(PS)+BS + sqrt(PS):BS	5		822.1	3.5	0.05
	sqrt(PS)		0.13 ± 0.04			
	BS		2.54 ± 1.02			
	sqrt(PS):BS		−0.08 ± 0.04			

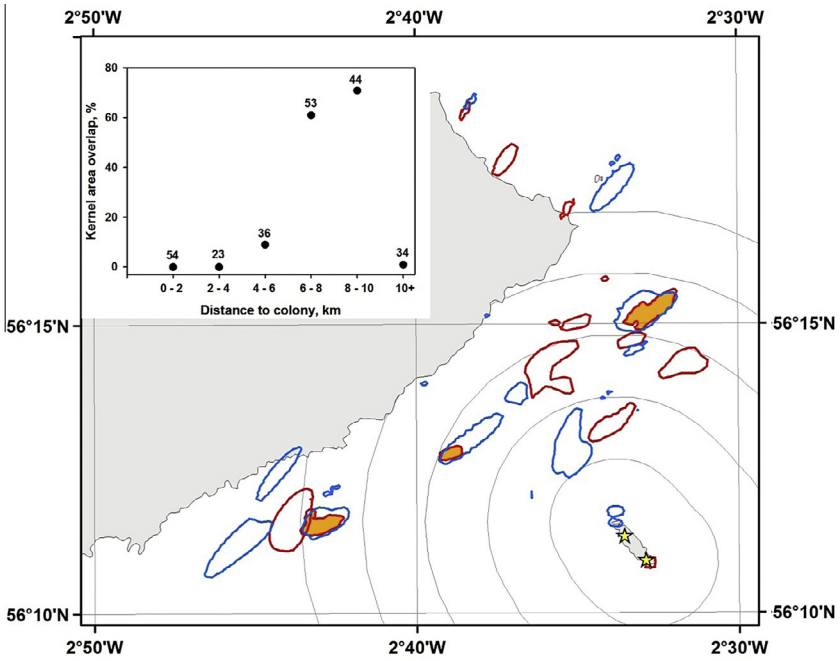

Fig. 4. Core foraging areas (50% kernel contours) of shags from the northern sub-colony (shown in blue) and southern sub-colony (shown in red) at different distances from the Isle of May; overlapping areas shown in orange; location of each sub-colony denoted by a star. Inset: overlap (%) of the core foraging areas of birds from the two sub-colonies in relation to distance from colony; sample sizes of tracked individuals shown for each data point.

entirely spatially segregated as birds foraged in areas adjacent to their respective sub-colony (Fig. 4). Segregation was also apparent at distances of 2–4 km, despite foraging distributions of the two groups both lying north of the island. In contrast, more distant foraging areas near the mainland coast, between 6 and 10 km from the colony, overlapped to a considerable extent (Fig. 4). Almost complete segregation was again observed in the most distant core foraging areas (over 10 km from the colony; Fig. 4).

4. Discussion

Using a 15-year tracking data set involving more than 300 individuals and 1100 trips, we identified important foraging areas of breeding shags over more than two decades during which environmental and intrinsic conditions varied considerably. Although three areas were used consistently throughout the study, significant interannual variation in distribution was apparent, such that 8 years of data were required to estimate over 90% of the population foraging area identified from our long-term study. However, with one and two years of data a substantial proportion of this area (54% and 64%, respectively) was captured. Furthermore, we identified interplay between extrinsic and intrinsic determinants of foraging range, such that range increased with population size when environmental conditions, as indicated by population breeding success, were poor but not when conditions were good. In addition, females had a larger foraging range than males. Finally, we demonstrated complex patterns of sub-colony admixing such that overlap in foraging distribution was greater at intermediate distances from the colony. Our results highlight the value of long term tracking studies in assessing the consistency of area usage over time and quantifying the duration of study required to adequately capture foraging distribution. They also demonstrate the importance of considering prevailing conditions and representativeness of the sample of the population studied.

4.1. Implications for the conservation of Isle of May shags

Despite variation in diet over the course of the study, there was no suggestion that diet composition had an impact on foraging range. In contrast, we found evidence for density-dependent effects that may be due to shags depleting or disturbing local prey populations (Birt et al., 1987; Lewis et al., 2001). The effects of population density were manifested mainly when environmental conditions were poor, supporting findings in a recent study (Davies et al., 2013). Population size and population breeding success varied by a factor of 4–5 over the course of the study, yet the foraging distribution of Isle of May shags has remained broadly similar. It is striking that our results match closely those presented in Wanless et al. (1991), based on the first three years of the study, and reflects that Isle of May shags feed benthically in spatially stable habitats (Daunt et al., 2003; Watanuki et al., 2008). Our analysis of the sample size of years required to estimate population distribution, coupled with the recent study by Soanes et al. (2013a) demonstrating the importance of within-year sample size, suggests that representative data may have been obtained from a 1–2 year study with large sample sizes. However, 1992 provides a cautionary tale. We now know that such years are rare, and re-analysis excluding this year showed that, because of the duration of our study, it did not have strong leverage on the results. However, a short-term study that included 1992 would have resulted in markedly different assessments of foraging distribution.

Of the three main areas used by Isle of May shags, the area surrounding the island is already designated as a seaward extension to the breeding colony SPA (Fig. 1; McSorley et al., 2003). Although the boundary of this designation was based on data from other species (auks and fulmar), it is encouraging that some foraging locations for shags lie within the SPA boundary and therefore the population is receiving some protection. However, the remaining two areas near the mainland coast are outside the SPA boundary and comprise just 23% of the triangular area of sea between the northern mainland and the Isle of May. Since shags are considered

to be more at risk from underwater structures such as tidal or wave energy developments encountered whilst foraging (Grecian et al., 2010; Langton et al., 2011) than those encountered in flight such as wind turbines, protecting key foraging areas could help safeguard the birds from such threats. However, the more distant areas such as those used in 1992 should not necessarily be ignored when considering locations for protection or development. Such areas may be important in enabling a population to survive poor conditions, and may become important in the future if habitats where the population is currently concentrated become unavailable or unprofitable.

Differences in foraging distribution were also recorded in relation to sex and sub-colony. Male shags are 15% larger than females (Wanless and Harris, 1993a), so sex differences may be associated with size dimorphism, as demonstrated in closely related species (Quintana et al., 2011). Disproportionate impacts of an underwater development on one sex could have important consequences for the population, since both members of the pair share breeding duties. It is increasingly recognized that birds from different colonies have discrete feeding areas (e.g. Wanless and Harris, 1993b; Grémillet et al., 2004; Wakefield et al., 2013). Our data showed that individuals from two sub-colonies exhibited at-sea segregation close to the colony and at the most distant feeding sites. Sub-colony variation in foraging areas has rarely been considered (but see Hipfner et al., 2007) and may be driven by energetic constraints, intraspecific competition for food, local knowledge or the use of visual information from mates or neighbors (Ashmole, 1963; Ward and Zahavi, 1973; Cairns, 1989; Weimerskirch et al., 2010). Such spatial segregation has important implications for estimating the proportion of the population being affected by anthropogenic developments or protected by MPA designation. For example, an underwater installation placed within 4 km of the Isle of May may only impact on a subset of the population, whereas one placed more than 6–10 km from the island may affect all sub-colonies. However, it would be worthwhile undertaking simultaneous deployments in a larger number of sub-colonies and years to gain a more complete picture of sub-colony segregation.

4.2. Wider implications

Our finding that with one or two years' data it may be possible to capture a considerable proportion of the long-term population foraging area is potentially important for the many studies aiming to identify population foraging area using short-term data. However, the number of years needed to adequately describe this area will depend on the extent of interannual variation in foraging distribution. Although the diet of shags in the UK and the rest of northern Europe is dominated by benthic species, in particular lesser sandeels (Wanless and Harris, 1993a), pelagic prey form a significant proportion of the diet in some locations (e.g. Swann et al., 2008), so the association of foraging locations with seabed substrate at those sites may be weaker. This may result in less consistency in the areas used among years and therefore a longer period of data collection may be required to estimate distribution. In contrast, fluctuations in shag population size in other areas, such as the UK's west coast, are much lower than those recorded on the Isle of May because population crashes do not generally occur (Swann, 2011), so fewer years of data may be needed to determine foraging areas because of less variation in density dependent effects.

These considerations are equally relevant for quantifying the foraging distribution in other seabird species. Our results may be most relevant to benthically feeding, coastal species such as other cormorants and auks. Despite differences in life history characteristics and ecology among seabird species, interannual and/or within-population variation in foraging distribution are likely to be apparent in many populations. The number of years of data collection needed to identify the distribution may therefore depend on variation in environmental conditions or density-dependent effects, such that more years' data would be required when conditions are more variable. In studies spanning few years, collecting data on parameters such as breeding success, population size and environmental conditions would help set the data in context, potentially identify atypical years (such as 1992 in our study) and inform decisions regarding further data collection. In addition, the number of years of data needed to estimate distribution may be reduced if large within-year sample sizes of individuals, trips and locations can be obtained (Girard et al., 2002; Soanes et al., 2013a). The optimal balance between sample sizes of individuals, trips per bird and locations per trip will depend on the extent of individual specialization in foraging behavior (Woo et al., 2008; Soanes et al., 2013b).

Differences in at-sea distribution of subsets of a population can determine what proportion of the population is affected by anthropogenic developments or protected by MPA designation. For example, segregation of foraging areas of different sub-colonies could result in small scale developments such as tidal and wave renewable installations only affecting a subset of the population. Similarly, when considering candidate MPAs, sub-colony segregation could be important in determining what proportion of the population is protected if boundaries are based on tracking data from a subset of the population. We therefore suggest that deployments are spread across the colony where logistically feasible. Sex differences in foraging range should also be taken into account as giving less protection to one sex in species with biparental care may impact disproportionately on the population. Tracking studies should therefore aim for a balanced sex ratio of tracked birds where possible. Although this is challenging in species which cannot be sexed in the field, molecular sexing is possible at some field sites so could be built into data collection protocols. One approach is to track both members of the pair, though this introduces nest-level non-independence which may be undesirable. An alternative approach is to collect sufficient sample sizes that ensure the probability of an imbalanced sex ratio is minimized.

4.3. Conclusions

Marine spatial planners are under pressure to simultaneously deliver sustainable economic development and conservation objectives, against a backdrop of substantial environmental change (Douvere, 2008). The impact of marine developments on higher predators is central to marine spatial planning, and tracking studies are playing an increasingly significant role in informing this process. It is therefore important to instigate protocols that maximize the representativeness of tracking data of the population in question. In addition to adequate sample sizes among and within years, consideration should also be given to temporal changes in distribution. Although not apparent in our study, such changes are a possible consequence of environmental change, necessitating ongoing data collection and highlighting the value of dynamic as opposed to static protection to safeguard populations over time (Game et al., 2009; Hobday, 2011). All of these issues are relevant to species conservation in general, since logistical constraints and challenging timescales are not just limited to marine spatial planning. Whilst we are not able to provide formal guidelines on how much data are needed, we consider it of paramount importance that species conservation plans aim to capture among-year and within-population variation in distribution to maximize the chances of long-term protection.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.12.025.

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